Barriers, contact zones and subspeciation in central equatorial Africa

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African forest and savanna avifaunas are recognised as being different, at least since Chapin's (1923) authoritative paper. Ecological vicariants do exist, but the number of biological species, composed of separate taxa, making contact in the forest/savanna border areas is restricted, *contra* Endler (1982). In fact, only few examples have been documented: e.g. *Scopus umbretta* (Bates 1931, Louette 1981), *Apaloderma narina* (Clancey 1959) and *Campethera caillautii* (Prigogine 1987). Similarly, the contact montane/lowland forest coincides very rarely with subspecies contacts: *Dendropicos elliotti* is one of the few examples (Louette 1981). There are, however, some superspecies contacts in both cases (see Prigogine 1980), but far less than Endler seems to admit.

In the present paper, we are concerned with examples to show differing contacts within the central lowland forest itself, the region from southern Cameroon to eastern Zaïre (Fig. 1).

The ranges of forest birds and savanna birds penetrating forest in equatorial Africa were mapped in the *Atlases* by Hall & Moreau (1970) and Snow (1978). Some additions were made by Snow & Louette (1981) and Louette (1984, 1987, 1988, 1988a, 1989). These and other papers cited should be used to illustrate the ranges of several birds given as examples below; but an incomplete positioning of contact zones between subspecies in Africa was given by Meise (1975) and by Mayr & O'Hara (1986) and a general examination of the ranges in order to identify possible barriers is long overdue.

Barriers and contact zones

Some African birds are able to leave their habitat temporarily (many Holarctic migratory forest birds, of course, do so): e.g. the long-distance migratory savanna nightjars *Caprimulgus rufigena* and *Macrodipteryx vexillarius* cross the forest twice after the breeding season, breeding only in the south. But there are almost no migratory African lowland forest birds.

I listed elsewhere (Louette 1990) the 216 stenotopic forest species. The selection was arbitrary. Here I want to mention that for some at least, the wrong decision seems to have been taken: *Telacanthura melanopygia, Neafrapus cassini, Eremomela turneri, Muscicapa tessmanni* and *Nectarinia cyanolaema* are indeed also forest birds, according to my own definition. Moreau (1966), Forbes-Watson (1970) and Amadon (1973) came to comparable figures. In any case, the degree of stenotopy varies within the group. I counted 156 stenotopic species covering virtually the whole forest block, leaving only a minority with restricted range therein. These contemporary ranges (and those of some other, eurytopic species) are

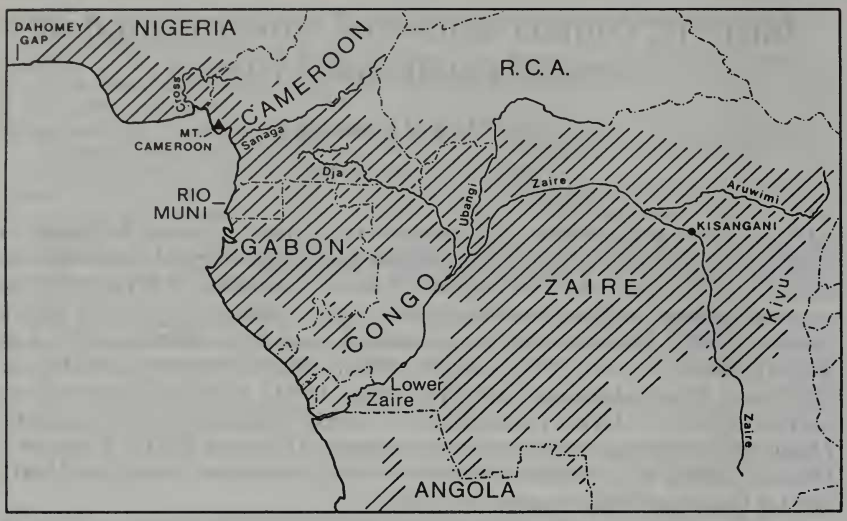

Figure 1. Central equatorial Africa. The Lower Guinea rainforest block is indicated with oblique barring.

considered to be positions taken up after radiation from a refuge and probably still dynamic (Mayr & O'Hara 1986). Suspected present day, as well as past, barriers (except for the presence of a vicariant species) include: degrees of altitude; inimical vegetation surrounding a refuge; savanna; hostile habitat in general: rivers and marsh. Examination of the ranges of such siblings as *Estrilda nonnula* and *E. atricapilla* allows one to presume that several such factors can act simultaneously (vicariants, philopatry, altitude, non-forest habitat, . . .).

Competition with other species cannot explain the peculiar distributions of the stenotopic forest birds (nor the eurytopic savanna birds mentioned below), because usually no congeneric species are involved. The polyspecific forest genera *Bleda* and *Malimbus* (the latter including 2 superspecies) were examined on this account, but no proof of competitive exclusion was found (Louette 1991a). However, the possibility of recent range restrictions or differences in ecological potential between the different parts of the forest cannot be excluded (Louette 1990). The restricted ranges are situated in particular areas outlined below, for which Louette (1990) produced a list of species (*pace* that given by Mayr & O'Hara 1986, which contains numerous errors, including the ranges for *Glaucidium sjoestedti, Spermophaga poliogenys, Merops breweri, Nectarinia adelberti* and others). These restricted ranges cover:

1) the whole of Upper Guinea or Lower Guinea, supporting the strong impact on distribution of the Dahomey gap in western Africa, a present day savanna wedge in the forest (Bates 1931, Moreau 1966);

2) particular parts of Lower Guinea in Cameroon/Gabon, in the Zaïre basin proper (only a few), and in a small eastern area;

3) the coastal forest for 3 species: *Tauraco macrorhynchus, Gymnobucco calvus* and *Nectarinia fuliginosa.*

There being no obvious ecological reason for this pattern and assuming those species under 2) and 3) did in fact have time and opportunity to spread out in the adjoining apparently suitable habitat, but did not do so, there must be a historical reason. The study of philopatry, with its genetic causes, is still in its infancy (Greenwood 1987). Land areas with high diversity and endemism correspond to refuges and centres of evolution during dry climatic phases according to several authors quoted by Prance (1982) and Crowe & Crowe (1982). Crowe & Crowe lacked information on the non-existence of an earlier suspected range gap for several bird species (such as *Apaloderma aequatoriale*) in central Zaïre (Louette 1984). Mayr & O'Hara (1986) and Prigogine (1988) again discussed the refuges for birds specifically in this region and Prigogine accepted a Zaïre Basin refuge which was not admitted by previous authors. Colyn *et al.* (1991), basing themselves on Primate ranges in the same region, similarly do not find a (geographic) diversity gradient, accepting also a quaternary (central) fluvial refuge, south of the present middle Zaïre. We lack, however, information on possible barriers in the period since the last dry phase.

Range limitation for forest birds by rivers

In South America, Capparella (1991) finds a whole series of bird species limited in range by large rivers (hundreds of cases?), or with separate subspecies or proven genetic differentiates on each bank. In central Africa, a similar phenomenon caused by several rivers was shown by Colyn (1987, 1988) for Primates. So it is reasonable to enquire whether this factor applies in African birds.

Very few subspecies ranges are given as delimited by rivers by White (1960, 1961, 1962, 1963, 1965), but that this could be the case for, for example, *Glaucidium tephronotum, Tockus hartlaubi* and *Alethe diademata* could be inferred. The maps in the *Atlases* for, for example, *Gymnobucco peli/sladeni, Trichastoma albipectus/cleaveri, Apalis rufogularis* races and *Anthreptes fraseri* races, also do give this impression for the Zaïre river, but the limitation is probably due to coincidence, in the same way as the range of *Ceratogymna elata* or the contact zone of *Malimbus cassini/scutatus* is limited by the Sanaga river (Louette 1981). In the *Tauraco persa* superspecies, where the Ubangi/Zaïre was a suspected barrier (Snow 1978), *persa* crosses it in fact towards the east in 2 places (Snow & Louette 1981).

There seems to be a genuine case in the genus *Centropus: C. neumanni* lives north and *C. anselli* south of the Zaïre river in Zaïre, but *C. anselli* also on the right bank towards Cameroon. In addition, *C. neumanni* does not reach the southern Kivu—it is definitely a philopatric species. (The other contact in the superspecies, *C. anselli/leucogaster*, in Cameroon and without introgression, is not along a river—Louette 1981). In investigating whether a coucal population would be limited by a very broad river, at least several hundred metres wide in the stretch of river considered and with a quite stable regime (Devroey 1951) and containing forested

islands, I found traces of introgression in the 'contact area', west of Kisangani, showing that the Zaïre river barrier is actually not absolute (Louette 1986).

Barriers by rivers seem to occur in African birds otherwise only in a few galliformes.

1)*Francolinus squamatus* and *F. ahantensis* are separated by the lower Niger (Elgood 1982).

2) *Guttera plumifera* is apparently squeezed by the Sanaga (Dejaifve 1991 mentions an unconfirmed sighting on the right bank) and the Zaïre rivers.

3) *Agelastes niger* lives from the Nigerian/Cameroon border in the west (Dejaifve 1991; limited by the Cross river?) to the right bank of the Zaïre (without penetrating towards southern Kivu).

4)*Afropavo congensis* has, in the opinion of all previous workers, a most puzzling range, present as it is on both banks of the Zaïre, but living in eastern Zaïre only. Verheyen (1962), suggested it is limited by the very humid soils in the western part of the Zaïrean (marsh) forest on the left bank, and by high altitude in the east. This may well be so; it is hard to believe that it would be excluded by the much smaller and even partly sympatric *Agelastes niger*, as suggested as plausible by Snow (1978). But why is it absent from the middle part of the right bank where the forest is 'dry', as in the bird's actual range (IUCN 1990)? Possibly these 2 species became trapped in pockets of forest on the 2 different banks of the Zaïre or Aruwimi rivers during a dry period, before spreading out and living now mostly, but not exclusively, on different banks.

The absence of both *Centropus neumanni* and *C. anselli*, and also *Agelastes niger* from the well forested southernmost Kivu suggests that this region was barriered from their refuge, configuration of the rivers perhaps prohibiting colonisation in this area by these 'philopatric' species avoiding large river crossings. To the contrary, *Afropavo congensis* was possibly on the right bank of the Zaïre, but later crossed it upriver from say Kisangani, penetrating to and beyond the left bank; it has crossed the Aruwimi as well (see map in Verheyen 1962).

It is noteworthy that other forest galliformes, in the genera *Guttera* and *Francolinus*, are not delimited by the entire Zaïre river. *F. lathami* shows a peculiar pattern of distribution, with the population in south-central Zaïre morphologically so similar to the one towards Cameroon/Gabon that it is considered consubspecific and different from the population more to the north in Zaïre, on the right bank of the Zaïre river (Louette 1984). This southern population must have arrived from the west (or *vice versa*), crossing the Zaïre river in its lower reaches, rather than arriving from the more plausible northern population; but the latter possibility may indeed have been excluded by the middle Zaïre river (or Ubangi river) being a barrier at the appropriate period. There are other examples of extension of races of strong flying lowland forest birds from western origin towards southern Zaïre or northern Angola or both, suggesting possibly simply another forest localisation formerly.

In contrast to Amazonia, it is clear that equatorial Africa does not have a river system separating bird populations to a great extent. A study of

the genetic differentiation of all these species on both banks would be welcome.

Particular savanna species delimited by forest

One wonders what would be the barrier in the species where the range includes a particular part of the forest, though the largest part of the range is in savanna; an example of this distribution of eurytopic species is *Buteo auguralis* (Louette 1991). It migrates to rather high latitudes in the northern hemisphere in Africa. However, it is present (only as a migrant?) in the whole forested region of Upper Guinea and from western Cameroon towards northwestern Angola; it is absent towards the east in central and southern Zaïre in forest as well as in the periforest/savanna, although there is no vicariant. Other species with a rather similar distribution are not rare: *Agapornis pullaria, Colius striatus, Centropus monachus, Smithornis capensis, Chloropeta natalensis, Zosterops senegalensis* and *Poeoptera lugubris*. The fact that these eurytopic savanna birds occur in 'the Cameroon/Gabon forest refuge' and not in 'the Zaïre Basin refuge', augments diversity there and explains in part Crowe & Crowe's (1982) findings. However, in my opinion these species do not really belong to the forest avifauna. Further, their absence in accessible savanna points to a historical reason (and philopatry) for the peculiar distribution. But there may be an ecological one—maybe they do not penetrate into marshforest or into the deepest part of the forest block.

Haffer (1988) estimates c. 100 land bird species in Amazonia are limited to riverine surroundings in forest. Such a group exists also in forested central Africa, but its composition in species is much smaller: *Pseudochelidon eurystomina* (migratory), *Riparia congica, Nectarinia congensis* and *Quelea anomala*. These live only alongside the Zaïre and its major tributaries, apparently enclosed by 'hostile habitat (forest)' and unable to escape to possibly more favourable habitat elsewhere; Prigogine (1988) incorporates them in his group originating in the Zaïre Basin refuge, together with real forest birds with restricted range. There is a possible second type in the forest: *Bradypterus grandis* lives in riverine marshes along the Dja river (it occurs also in Gabon). Possibly an almost unknown species such as *Ploceus batesi* will reveal itself as also being confined to riverine forest habitat. Other typical riverine birds such as *Ploceus melanocephalus duboisi, P. pelzelni* and *Merops malimbicus* are not completely enclosed by the forest block, although they are restricted in range to central Africa. In addition there are other riverine species in central Africa, but surrounded by savanna (outside the scope of this paper), suggesting that the forest is a barrier by chance for the riverine group. Similarly, *Anthreptes gabonicus* and *Ploceus subpersonatus* are limited to mangroves, the last one to a very restricted part of them.

That forest can be a solid barrier is proven indirectly by the stenotopic savanna bird penetration from the northern woodland and savanna through a (former) corridor along the Ubangi river towards Lower Zaïre, such as *Dendropicos goertae* (Louette & Prigogine 1982). Other similar cases are *Numida meleagris, Caprimulgus climacurus, Crinifer piscator, Phoeniculus aterrimus* and *Batis minor* (Louette 1987). No differentiation, or only minor, has occurred suggesting recent immigration.

The surroundings of the lower Ubangi were even contemporarily not covered with forest, large 'ésobé' grasslands existing in this general area. These species definitely must have followed a western (central) route, because east of the forest belt the savanna connection is blocked by a vicariant. There are no examples of a penetration northwards (but possibly they would spread out rapidly and cannot be detected by examination of range maps). The last arid period seems to have culminated at 18,000 years BP (van Zinderen Bakker 1986), with semi-arid conditions in the 'central Congo' region. The aridity was of a magnitude much larger than needed to explain these penetrations, permitting a whole savanna fauna exchange. Probably *Francolinus coqui* (towards the north) and *F. albogularis* (towards the south) achieved the penetration during such a period. The present positioning of the savanna species in Lower Zaïre must have taken place much later (the equatorial forest reappeared from 9000 years BP—Maley 1989), with a corridor of grassland as a sufficient gateway. Also, the separation of the forest bird populations referred to above as being possibly due to the Zaïre river may simply have been produced by this vegetation corridor along the river, not by the river itself.

Subspeciation

Subspeciation within the Lower Guinea forest block proper is given in White's check-lists. He does not differentiate races based on colour or on measurements, nor abrupt and clinal ones. Since White's papers were written, no complete review of subspeciation in Africa has been made. Therefore we still use White's races provisorily to render geographical variation, although, no doubt, in many cases too few statistically valuable criteria were used to create them (see Barrowclough 1982).

Contacts between subspecies of forest birds, as for borders of species' ranges, are numerous in the general region of Mount Cameroon, clearly a suture line of an old non-forest gap (Louette 1981; but see Maley 1989, who postulates montane forest descending to lower levels here during part of the Quaternary). Some of the contacts are somewhat to the west, others to the east of Mount Cameroon (cf. Meise 1975), quite possibly a result of different colonisation speed rather than an indication of separate gaps (cf. Mayr & O'Hara 1986); also, the supposed influence of the Sanaga river may in fact be a consequence of this Mount Cameroon gap. Examples rather far to the east from the Mount Cameroon suture line include: *Lybius hirsutus, Pitta angolensis* and *Stiphrornis erythrothorax*. With the contact still more to the east is *Terpsiphone rufocinerea*, studied by Chapin (1953); equally *Alcedo leucogaster, Bycanistes fistulator, Psdalidoprocne nitens* and *Alethe poliocephala* qualify. Some western races are present in northwestern Angola, but for *Spermophaga haematina* the eastern race is there and I suggested a "push" from the western population in the southern Zaïre sector towards the east (Louette 1988). Subspecies bordering the Zaïre river were mentioned above. A former gap (savanna, ésobé grassland, lake, river?) in west-central Zaïre may explain these positions.

Clines in colour or dimensions or both are present in many forest birds, with the gradient changing from west to east somewhere in Zaïre (Louette

1991a gave several examples: e.g. *Andropadus latirostris, Bleda syndactyla* and *B. eximia*). (Others are morphologically homogenous throughout this part of the range, though differing elsewhere; for example *Andropadus virens*.)

The morphological differences in bird species in Lower Guinea (just as are those for Upper Guinea, listed by Bates 1931) do not contradict the refuge hypotheses. The contacts between (incipient) subspecies in Lower Guinea may be the result of both an east and a west colonisation from the Cameroon-Gabon and Albertine Rift refuges (which other species due to philopatry are still occupying solely—Crowe & Crowe 1982, Prigogine 1988). Possibly, however, some of the differentiation is due to adaptation to local conditions: the study of this phenomenon is far from finished (Boag & Van Noordwijk 1987).

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